

Territorial Behavior of the Red Admiral, *Vanessa atalanta* (L.) (Lepidoptera: Nymphalidae)

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Although butterflies are not equipped with means to inflict injury, the intensity with which males of many species pursue conspecifics, butterflies of other species, birds and even lepidopterists suggests that some butterflies are highly aggressive (Silberglied, 1977). Recently there has been an increasing number of reports that the apparently aggressive behavior of some species is part of territorial behavior (Baker, 1972; Douwes, 1975; Silberglied, 1977; Davies, 1978).

Scott (1974) suggests that butterflies are not aggressive and not territorial. He believes that what appear to be aggressive attacks are simply males' attempts to determine the species and sex of flying objects perceived from a perch. Because male butterflies do not always return to the same perch and usually do not occupy the same perch on successive days, Scott questions whether male butterflies of any species occupy fixed areas.

In this study, we described behavior of *V. atalanta* males which we believe represents true territorial behavior, namely defense of a fixed site.

Materials and Methods

Observations were carried out at various locations on the Iowa State University campus. Butterflies of the spring brood¹ were observed on 8 days between May 4 and 17, 1977, 8 days between May 18 and 26, 1978, and 8 days between June 9 and 21, 1978. Butterflies were identified by unique characters (raggedness of wings, size, color) and by marking descaled areas of one wing's ventral side with spots of non-toxic acrylic paint. Thirty-six territorial butterflies were captured and sexed by gently squeezing the tip of the abdomen to extrude the genitalia. After sexing and/or marking, captured butterflies were released under the net and gently directed to the ground or sidewalk near the resting spot of capture. However, 41 of 43 males flew away immediately after release.

¹ In 1978, the first adult butterfly was spotted on May 18 and the last territorial male was seen on June 26. Within 2 weeks, we again saw adults, apparently members of a summer brood.

Results

Although individual *V. atalanta* were observed flying through territorial sites as early as 0900 hr, territorial behavior was never observed earlier than 1700 hr (CST). Within 30 min after the first territory was established, the number of territories increased and their boundaries became sharply defined. Intermittent flights (patrols) by territory occupants traced territorial boundaries (Fig. 1). Boundary lines were confirmed by points at which butterflies stopped pursuing floating objects, birds and other species of butterflies. Males usually occupied territories until 1830-1930 hr but left earlier on cool or overcast days.

Usually one male occupied and successfully defended his territory for a 2-2½ hr period. Since marked males almost always flew away immediately after release, discrimination between occupant and intruders depended on our ability to identify unmarked butterflies. In eight cases (which included two previously marked butterflies), we could easily identify the original resident of a territory and determine whether these butterflies successfully defended their territories for the total daily territorial period, or were displaced. In six cases, the initial occupants were not displaced; each occupant drove off one to 13 intruders. The other two males eventually lost their territories to intruders. One male was displaced after his third flight interaction with an intruder. The other male defended his territory successfully eight times before being driven off during his ninth flight interaction.

Different males tended to occupy the same territories on different evenings and even during different years. Butterflies occupying a territory on a particular day rarely returned at a later date. Of 39 individually identified males (35 marked, four identified by unique morphological characteristics) in 1977 (nine males) and 1978 (30 males), only two males returned to the same or adjacent territories on subsequent evenings.²

Territories were roughly elliptical in shape, varying from 12-24 m in length and 4-13 m in width (Fig. 1). Each territory had a core area, an area common to a territory mapped on successive days (Fig. 2). The area peripheral to the core area varied with different territorial

² Both males returned under unusual conditions. One male, marked on May 23, 1978, roosted in a tree within his territory. This was the only male ever seen to roost in a territory. He was observed the next morning at 0900 hr, had departed by 1000, and returned to the territory by 1730.

The other male was marked in territory #1 on June 9, 1978. He was seen in territory #1 on two different occasions on June 19, 1978 for periods of 2 and 10 min before being displaced. This male reappeared in territory #1 only after at least eight former territorial owners had been marked and fled the territory.

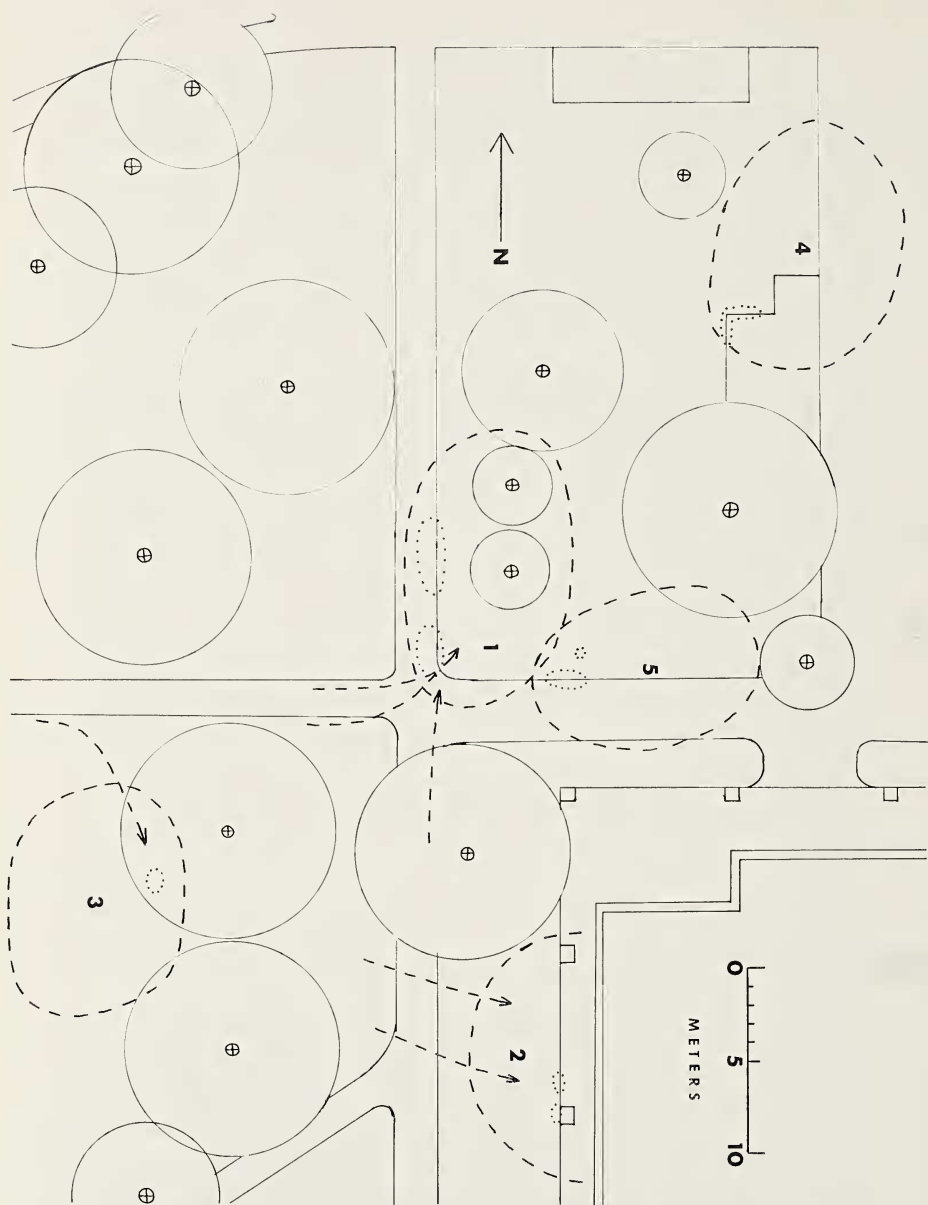


Fig. 1

Territories in courtyard on ISU campus, May 1977. Dashed lines - typical, territory boundaries. Dotted lines - shape, size and location of resting spots within territories. Arrows - routes along which intruders frequently entered territories. Solid lines - trees, sidewalks, buildings.

owners. In some cases, even the peripheral areas were similar for two or more different territorial owners.

Each territory contained one or two fixed resting spots which lay within core areas and were similar for all territorial holders of a given territory (Figs. 1, 2). Not only did each territorial owner consistently return to the same spot, but intruders capturing that territory on the same night, and occupants on successive nights (even successive years) rested on approximately the same spot. Resting spots were usually on the ground (sidewalk, rocks, or patches of bare ground), occasionally on the walls of buildings, or, less often, on a bush or low branch of a tree. Resting spots on sidewalks were ellipses 1-2½ m long, 30-60 cm wide with major axes parallel to the long axis of the sidewalk. Butterflies spent 70-90% of their time resting within their territories. Resting spots on walls were 30 cm to 2 m in diameter, located 30 cm to 3.7 m up the wall. Except when interactions were unusually frequent, butterflies spent 70-90% of their time resting within their territories.

Territories were found along sidewalk edges, along sunlit, western-facing walls and on open sunlit lawns (Fig. 1). The major axes of some territories pointed toward trees or corners of buildings lying some distance from the territories.

Normally *V. atalanta* males spent 4-12% of their time patrolling their territories, flying 7-30 patrols/hr. However, one male occupying a territory on an open sunlit lawn patrolled continuously for the last 1¼ hr of his territorial period. During a single patrol, a male traced a flight path two to six times in a period of 5-60 sec before returning to his resting spot. Butterflies usually patrolled along the edge of a territory about 1½ m above the ground. One butterfly occupying territory #2 (Fig. 1), repeatedly climbed approximately 9 m up the wall in a winding fashion.

When large objects (white cloth bag, spiral notebook) were placed within territories, patrolling butterflies changed course and repeatedly flew around these objects. Sometimes butterflies hovered above objects or perched on them briefly before resuming patrolling or returning to their resting spots. During June 1978, workers dug a hole within the core area of territory #1 (Fig. 1) and placed a fence around it. Butterflies avoided the fence and territorial boundaries were restricted to within a meter of the edge of the sidewalk.

Some territories may be considered optimal because of considerably greater frequency of occupancy. Frequency of occupation of each territory was similar during 1977 and 1978. During a total observation

period of 20 days in May 1977 and May and June 1978, percentage of occupancy was 85% for territory #1, 60% for territory #2, 25% for territory #3, 20% for territory #4 and 15% for territory #5. Territory #8, observed for 12 days during May and June 1978, was occupied 83.3% of the time. Territories #1, 2 and 8 were preferred areas and therefore optimal.

The highest rates of resident-intruder interactions (up to 21/hr) occurred in optimal territories. Such competition occasionally resulted in two or more males claiming the same territory. A butterfly claimed a territory if he rested within that territory and flew or attempted to fly a pattern which defined territorial boundaries. When more than one butterfly rested in a territory, an occupant who flew up, presumably in an attempt to patrol his territory, was immediately chased by another occupant. The results of such competition were 1) establishment of an adjacent territory (two cases, Fig. 2), 2) splitting of a territory into two smaller territories (three cases, Fig. 3), 3) one butterfly was driven off (occurred only once), and 4) intermittent chases occurred until all butterflies flew away at the end of the daily territorial period (two cases). It is likely that occupation of any suboptimal territory (e.g., territories #4 and #5, Fig. 1) was a result of competition for a nearby optimal territory (e.g., territory #1, Fig. 1).

Territorial butterflies spent 5-15% of their time interacting with other individuals entering their territories. The rate of interaction ranged from 1.62-21/hr, but was commonly between 10-15/hr. Intruders typically entered a territory along specific routes, usually from the west (Fig. 1), flying from 30-130 cm above the ground (Fig. 4). The resting or patrolling butterfly then flew up or changed course, rushed at the intruder from underneath, and sometimes hovered above the intruder for 1-2 sec before chasing it along an erratic path 1-2 m above the ground for 5-20 sec. Sometimes the butterflies flew through the dense foliage of low branches. Then the territorial butterfly closed to within 30 cm of the other and began chasing it along one to seven turns of an ascending helical path, 4-9 m in diameter, most often in a counterclockwise direction as seen from below. When they had climbed to treetop level, some 10-18 m above the ground, the territory holder broke off the chase and dropped into its territory (Fig. 4). With close observation of chaser, we were able to distinguish territory owner from intruder an estimated 95% of the time. These interactions usually lasted 10-30 sec but some were as long as 60 sec.

After a chase, the intruder usually was lost from sight. When observed, the intruder usually flew a short distance from the top of the

helix before descending toward the ground and flying away. During frequent male-male interactions (10-21/hr), 5-8% of the intruders descended within a few meters of the territory and re-entered it immediately. During periods of high interaction frequency, an intruder may enter a territory while the owner is chasing another butterfly. We saw this three times in territory #2 (Fig. 1) on May 5, 1977.

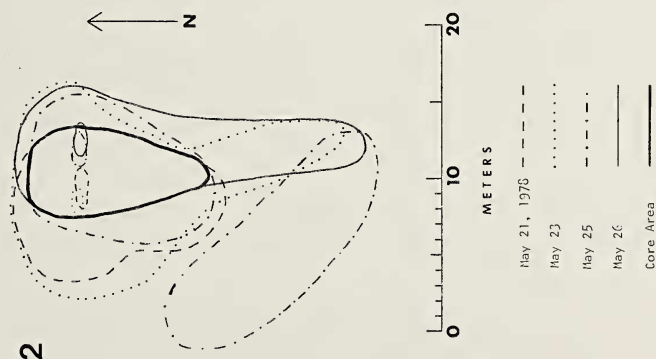
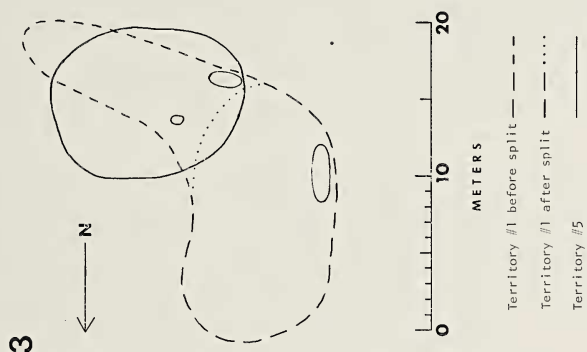


Fig. 2. Core and peripheral areas of a territory (#8). Adjacent territory occupied by second butterfly on May 25, 1978.

Fig. 3. Splitting of a territory as a result of competitive interactions of two males. Small ovals within territories are resting spots.

The frequency and lag time of reoccupation of a territory after release and departure of marked males is a measure of the availability of males without territories and possibly the intensity of competition for optimal territories. On June 19, 1978, we captured and marked, or chased away, 18 males in territory #1 (Fig. 1) between 1305 and 1910 hr. All males were replaced within a few sec. to 5 min. and only one replacee was a returnee marked 13 min. earlier in the same territory.

No *V. atalanta* were seen to feed, roost (one exception under unusual circumstances), oviposit or mate in defended territories. *V. atalanta* is not sexually dimorphic and all individuals that we sexed were males. We observed few behaviors, other than resting, chasing intruders and patrolling, which could be used to speculate about the function of *V. atalanta* territories.

Intermittently males opened their wings holding them in a horizontal position revealing the brightly colored dorsal side. This could be an aggressive or courtship display. Although no data were recorded, it appeared that males in sunspots held their wings horizontally more frequently than males not on sunny resting spots. This suggests that *V. atalanta* males may open their wings to help maintain or raise body temperature.

Discussion

According to Baker (1972), the nymphalid butterflies *Inachis io* and *Aglais urticae* establish breeding territories along visual lines of demarcation (i.e., hedges, walls or rows of trees) along which females are likely to fly. The most active (optimal) territories of *V. atalanta* were along sidewalks and sides of buildings which probably form strong linear visual patterns to flying butterflies. A line of two or more trees may have been necessary visual input for butterflies forming territories in open areas of the university lawn. Flight paths of intruders were similar for a given territory, suggesting that intruders were using the same visual orientation cues and probably the same used by the territory owner.

The locations of territorial resting spots and flight paths demarcating territorial boundaries probably also depend upon visual cues. Occupation of the same territories, same resting spots and, in some cases, similar territorial boundaries by different butterflies on different days (even different years) is strong circumstantial evidence for a species response to visual cues. *V. atalanta's* responses to foreign objects (hovering above, perching upon or flying around them) suggests they became familiar with visual features of their territories.

Visual cues also appear to be important in the territorial behavior of dragonflies. As with resting spots of *V. atalanta*, perch sites of males of the dragonfly, *Hetaerina americana*, tend to be permanent. Territory owners and intruders that succeed in displacing owners generally rest on the same perch (Johnson, 1962).

Resting spots (sidewalk, rocks, bare spots of ground) of *V. atalanta* are invariably lighter than the immediate surroundings. This also may be true for *Vanessa annabella* Field (Dimock, 1978). The choice, by *V. atalanta* males, of such specific areas for resting spots suggests use of visual signals other than lightness of background. A light background probably camouflages resting males with wings held vertically. The same background would contrast with and enhance the possible display of the colorful, horizontally-held wings.

Fixity of resting spots may be related to intruders entering territories from specific directions. If intruder's flight paths are determined by certain visual features of territories, those territory holders which establish resting spots near these entry points would force intruders to pass through the most heavily defended parts of the territory thereby reducing the intruders' chances of occupying it.

Although most resting spots of *V. atalanta* remained fixed during the entire daily territorial period, a few butterflies changed their resting spots in order to occupy a spot of sunshine. The butterfly *Parage aegeria* also remains in moving sunlit spots on the forest floor (Davies, 1978). For *P. aegeria*, however, the sunspot is the territory. *V. atalanta* males only occupied sunspots within their territorial boundaries and only when the temperature was below 20° C. Changing resting spots in order to remain in sunlight at relatively low temperatures may be a mechanism to prevent heat loss.

V. atalanta's attacks on a variety of animate (including other species of butterflies) and inanimate objects (e.g., floating leaves) suggest that their chase response is not very specific. Although *V. atalanta* males do not chase birds or other species of butterflies in a vertical helix, they do pursue them to the territory's edge with obvious intensity darting around them and moving toward them repeatedly as if attacking. This apparently contrasts with territorial *P. aegeria* males (and males of many perching species; Scott, 1974), whose approaches to other species of butterflies are described by Davies (1978) as inspections.

Although such intense chasing of other species of butterflies seems a waste of energy, selective factors other than energy savings from

chasing only conspecifics may be operating. The persistence with which a territorial *V. atalanta* chases a wide range of flying insects and birds could serve to 1) identify conspecifics and possibly sex of conspecifics, and/or 2) increase the rate at which birds and other insects leave the territory. If resting *V. atalanta* males cannot identify conspecifics, chasing off flying animals which they cannot differentiate from conspecifics should reduce their chances of chasing the same animal again. It is also possible that there have been, and may be in other areas, interspecific competitors for similar territorial sites. For example, Dimock (1978) reports that three species of *Vanessa* "congregate" on hilltops and other open sunny places where they chase one another along with unrelated butterflies, birds and other large insects.

The frequent interaction of two to five butterflies in optimal territories on sunny days, splitting of optimal territories or formation of adjacent suboptimal territories, and the rapid replacement of displaced territorial males, suggest that, at least on certain days, there is a low density of optimal territories. We have located only 10 territories on the ISU campus and no more than five are optimal. When optimal territories are limited, a non-territorial owner may occupy a suboptimal territory or contest for an optimal territory. Either strategy may result in approximately equivalent chances of obtaining a female (Parker, 1970).

Baker (1972) observed that, unlike *V. atalanta*, territorial *I. io* and *A. urticae* do not drop back into their territories after chasing intruders in a rapidly ascending spiral, but go into a series of dives and climbs along a path that carries them as far as 200 m away from the territory. In one respect, the long flight away from the territory is more advantageous than the helical interactions of *V. atalanta*, in that intruders would be less likely to find the territory again after chasing intruders in a rapidly ascending spiral, but go into a series of dives and climb along a path that carries them as far as 200 m away from the territory. In one respect, the long flight away from the territory is more advantageous than the helical interactions of *V. atalanta*, in that intruders would be less likely to find the territory again after having been chased off. However, such chases require the butterfly to spend time far from its territory, increasing the chances of a third butterfly occupying it.

The 10-18 m high helix of *V. atalanta* allows the territory holder to chase the intruder a relatively great distance upward without moving a large horizontal distance from its territory. If a third butterfly attempts

to occupy the territory, the owner can (and did) break out of the chase, drop downward, and rush at the new intruder. At the same time, the first intruder may become disoriented in overhead branches. Perhaps interaction type is related to the habitat the butterfly occupies. In open areas, such as the fields where *I. io* and *A. urticae* set up territories (Baker, 1972), the long flight away from the territory might be more advantageous, while in areas with tree canopy, the helix may be preferable.

Baker (1972) reports that *I. io* and *A. urticae* males feed in the morning, set up territories in the afternoon (1130-1630 hr), leave territories to follow females, and mate at an evening roosting site. This behavioral time table very likely applies to *V. atalanta*. We have observed lone and aggregated *V. atalanta* feeding at various locations around Ames, Iowa between 0900 and 1700 hrs. Although we have observed no activity other than resting, patrolling and chasing, some chased intruders may have been females and males chasing them may not have returned to their territories. When helical chases were carefully observed, one male, probably the territorial owner, was seen to drop back into the territory in 95% of the chases. In the remaining 5% of the observations, males could have followed females rather than returning to their territories.

In the few reports of nymphalid males chasing females (Temple, 1953, Stride, 1956), the butterflies hover or quiver together before the male chases the females in a rapidly ascending spiral. Stride (1956) describes quivering of male and female *Hypolimnys missippus* (L.) before and throughout an ascending flight. We observed hovering on only two occasions, repeatedly during flight interactions within territory #9 on May 26, 1978 and within territory #2 on June 13, 1978. According to Temple (1953) *A. urticae* males chase females in ascending spirals and the flight paths of each sex are different. In *V. atalanta*, the flight patterns of the two or three butterflies ascending in a spiral or helix are always the same. It is possible that all helical chases we observed involved only males.

Like *V. atalanta*, most males of *I. io* (Baker, 1972) and two species of *Hamadryas* (Nymphalidae) (Ross, 1963) probably occupy territories or perches for one day or less. According to Baker (1972), *I. io* males move across the countryside, in a more or less straight line, from one feeding site to another until about midday when they select a suitable territory. *V. atalanta* males also seem to move a great deal while feeding. Such movement would result in males occupying territories in new locations each day, which is consistent with our observations.

Scott (1974) suggests that before a butterfly species can be considered territorial "1) many males must remain at the same spot for a period of several days (also implied by Ross, 1963), 2) males must be able to quickly distinguish males from females, and 3) males must by intent drive other males from the area."

Noble's (1939) definition of a territory as a "defended area" has been restated by Brown (1975) as "... a fixed area from which intruders are excluded by some combination of advertisement ..., threat, and attack." This definition does not include Scott's (1974) requirement of territory occupation for "several days." *V. atalanta* males occupy and repeatedly defend (up to 21 times/hr) specific areas for periods up to 2 ½ hr.

Scott (1974) is critical of previous studies because they do not convince him that males consistently return to the same perch. *V. atalanta* territorial owners do consistently return to the same perch (resting spot). In addition *V. atalanta* males identify territories larger than resting spots by 1) outlining territory boundaries during numerous patrols, and 2) stopping at these boundaries when chasing birds or other butterfly species.

Scott's other two criteria deal with territorial defense. He believes that perched males pursue conspecifics and other flying animals, not to drive them from the territory, but to identify species and sex. However, Temple's (1952) description of courtship interaction of *A. urticae* is very different from Baker's (1972) description of territorial chases in the same species. This suggests that *A. urticae* males are able to distinguish an intruder's sex early in an interaction. Initially *V. atalanta* males sometimes hover and then chase an intruder along an erratic path. We suggest that sex and species recognition take place at this time after which the territorial male may 1) repeatedly dart at birds or other species of butterflies until they leave his territory, 2) chase inspecific males, and possible inspecific females, in a helical path, or 3) perform a yet undetermined flight path with a receptive female.

The evolution of territorial behavior in butterflies or any other animal is the result of increasing competition for access to one or more resources. In the case of butterflies, increasing competition for perching sites favorable to interception of females could lead to an increasing tendency to occupy specific areas and reduced time for species and sex recognition. Earlier sex and species identification would enable the territorial occupant to perform the behaviors appropriate to the type of intruder (e.g., driving conspecific males

away in a vertical path) and return as quickly as possible to reoccupy his territory. Scott's (1974) unwillingness to accept territorial behavior in butterflies probably results from his experience with perching species whose behavior lies along the continuum between species that occupy many poorly defended perches in poorly defined areas and species whose behavior approaches but is not truly territorial. We believe that *V. atalanta* male exhibit territorial behavior because they occupy and defend fixed sites.

Summary

Vanessa atalanta (L.) males maintain territories during a 2-2½ hr period before dusk. A single male usually holds a territory during the territorial period but may be displaced by an intruder, especially after successive interactions. Territory owners seldom return on successive evenings. *V. atalanta* males probably move varying distances while feeding during the day and set up territories in different areas each afternoon.

The location, shape and components of territories are probably established with respect to visual features of the environment. Territories are established along strongly linear features (sidewalks, sides of buildings, possibly a line of two or more trees). Territorial boundaries, roughly elliptical in shape, are defined by intermittent flights or patrols. Territory owners occupy resting spots, within the territories, which are always lighter (bare ground, sidewalk, sunspot) than the surrounding area.

Each territory has a core area, an area common to a territory mapped on successive days. For each territory, the area peripheral to the core area may vary among territorial owners, but even the peripheral area may be similar for two or more territorial occupants. Within each territory core area, there are one or two resting spots or perches. The same spot(s) were used by all territorial owners observed during spring 1977 and 1978.

Territory owners leave their resting spots and intercept other butterflies when the intruders cross the territorial boundary. Territorial butterflies chase intruders along an ascending helical path above the territory. Birds and butterflies of other species are chased horizontally and only to the territorial boundary.

Some territories are occupied much more frequently than others. Such optimal territories are intruded upon frequently and intruders, after being chased away two or more times, may return and rest in the territory. Such competition for an optimal territory may result in 1)

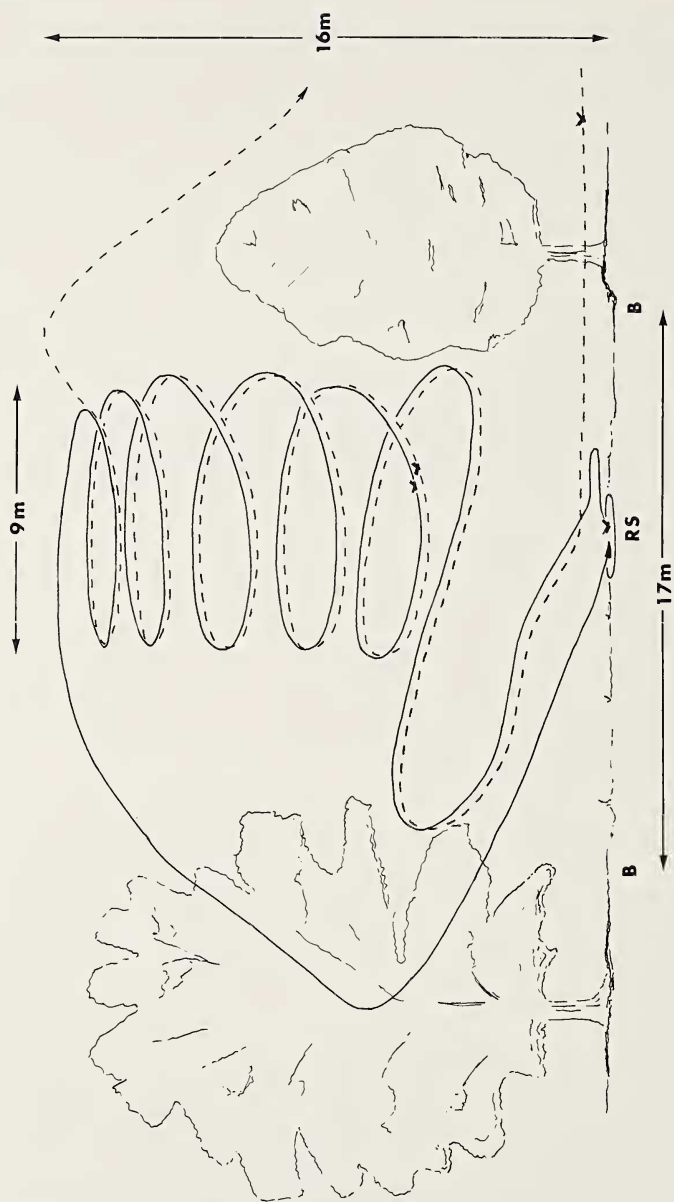


Fig. 4 Flight patterns during a typical interaction between two *V. atalanta* males. B — territory boundary; RS — resting spot; solid line — flight of territory occupant; dashed line — flight of intruder.

splitting of the territory into two smaller territories, 2) establishment of an adjacent territory, or 3) continued interaction until all butterflies leave at dusk.

The intensity of competition for optimal territories as well as rapid replacement of territorial owners driven from their territories suggests a low density of optimal territories. Territorial splitting, development of territories adjacent to optimal territories, and joint occupation of an optimal territory probably represent successful strategies of males who are not initial territory owners and who have failed to displace a male from an optimal territory.

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